

ANNUAL AND SPATIAL VARIATION IN SEEDFALL AND SEEDLING RECRUITMENT IN A NEOTROPICAL FOREST

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Abstract. An economy of scale may lead to selection to increase interannual variation in seed production when the per seed probability of seedling establishment increases with seed production. Variable annual seedfall will, however, reduce this probability when post-dispersal seed fate is negatively density dependent on the local density of seeds, and seed dispersal and density dependence act identically across years. Intuitively, more variable annual seedfall causes the representative seed to experience a greater density of conspecific seeds and suffer greater density-dependent effects. This handicap must be overcome for the per seed probability of recruitment to be greater in years with greater seed production.

We quantified spatial and annual variation in seedfall and seedling recruitment, evaluated density dependence and economies of scale during the seed-to-seedling transition, and investigated the synergistic consequences of density dependence and variable annual seedfall for seedling recruitment on Barro Colorado Island (BCI), Panama. Weekly censuses of 200 0.5-m² seed traps documented seedfall for 15 years and 108 plant species. Annual censuses of 600 1-m² seedling plots documented recruitment for nine years and 32 species. The density of seedling recruits tended to increase with the density of seeds; however, the per seed probability of recruitment invariably decreased with seedfall density. Negative density dependence characterized the seed-to-seedling transition. Observed levels of spatial and interannual variation in seedfall density would reduce long-term recruitment by up to 28% if negatively density-dependent survival acted identically across years; however, the strength of negative density dependence varied significantly among years for 12 of 32 species. Negative density dependence occurred in all years for these species but was significantly weaker during the one or two years of greatest seedfall than during the remaining years of lower seedfall. The per seed probability of recruitment increased significantly with annual seedfall for eight of these species. These eight species realized postdispersal economies of scale despite the reduction in long-term recruitment expected from the synergism between variable annual seed production and negatively density-dependent seed fate.

Key words: Barro Colorado Island; density dependence; lianas; masting; Panama; pest satiation; seedling recruitment; seed production; tropical trees.

INTRODUCTION

Population-level seed production varies widely among years in many plant species and is relatively constant in many others (Kelly and Sork 2002). This interannual variation has important implications for population, community, and ecosystem dynamics; for example, it can drive large population fluctuations of seed and fruit consumers and species with which they interact (Jones 1998, Wright et al. 1999). Current understanding of the causes of observed levels of interannual variation centers on three classes of hypotheses (Kelly 1994). Seed production may track or match variation in a limiting resource (the resource-matching hy-

pothesis). Alternatively, natural selection may act to increase or decrease interannual variation. Natural selection may favor variable seed production when large seed crops are timed to anticipate future environmental conditions that favor reproductive success (the resource prediction hypothesis), or when large seed crops themselves cause disproportionately large increases in reproductive success (the economy of scale hypothesis). In either case, enhanced recruitment following large reproductive efforts must offset opportunities for recruitment lost in years when the reproductive effort is curtailed, in order for natural selection to favor variable seed production or to increase interannual variation (Waller 1979).

Much attention has focused on the economy of scale hypothesis (Silvertown 1980, Herrera et al. 1998, Kelly and Sork 2002). Possible mechanisms that might lead to an economy of scale include the facilitation of wind pollination, the attraction of animal mutualists leading to increased pollination or seed dispersal, and the sa-

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TABLE 1. Studies of interannual variation in seed production and predation.

Predation timing/ plant part	Principal predator	Economy of scale [†]	Source
Predispersal predation			
Developing seed	insect	yes	Crawley and Long (1995)
	insect	yes	DeSteven 1982 (1983)
	insect	yes	Gardner (1977)
	insect	yes [‡]	Kelly and Sullivan (1996)
	insect	yes	McQuilkin and Musbach (1977)
	insect	yes	Nilsson and Wästljung (1987)
	insect	yes	Shibata et al. (1998)
	insect	yes	Shibata et al. (2002)
	insect	yes	Spere (1997)
	rodent	opposite	DeSteven (1982)
Postdispersal predation			
Dispersed seed	small mammals	opposite	Gardner (1977)
	vertebrates	yes	Nilsson and Wästljung (1987)
	rodent	null	Schupp (1990)
	rodent	null	Shibata et al. (2002)
	rodent	yes	Wolff (1996)
Seedling recruitment	rabbit	yes	Crawley and Long (1995)
Saplings	rodent	yes	Jensen (1985)
	none identified	null	Hett (1971)

Notes: Economies of scale, in which larger seed crops experience lower levels of predation, were found in all studies where the principal predator was an insect that attacks developing seeds, and in just four of nine studies where the principal predator was a vertebrate or attacked after seed dispersal. Each study compared predation for at least two years with different levels of seed production. The original author identified the principal predator.

[†] “Yes” and “opposite” indicate that predation was significantly lower and higher in years with greater seedfall, respectively. “Null” indicates that the null hypothesis of no difference in predation with seedfall was accepted.

[‡] Predation declined with the ratio of floret production for the present to the previous year.

tiation of animal pests leading to increased survival of flowers, seeds, or seedlings following large reproductive efforts (Kelly 1994). Of course, if large reproductive efforts have the opposite effect and satiate mutualists or attract disproportionate numbers of pests, then selection may act to favor constant seed production or to minimize interannual variation.

These considerations suggest that interannual variation in seed production should vary geographically. Kelly and Sork (2002) reasoned that seed production should be relatively constant among years in the tropics because (1) low climate variability minimizes resource variation, (2) high tropical productivity minimizes the time required to recover resources after large seed crops, (3) high plant species diversity makes it difficult for any one species to satiate generalist seed predators, and (4) most plant species are pollinated and have their seeds dispersed by animals, whose numbers and services would be adversely affected if host reproductive effort was highly variable. Interannual variation has rarely been quantified in the tropics, and Kelly and Sork (2002) were unable to evaluate their hypothesis convincingly because their exhaustive review of the literature, which documented patterns for 579 plant populations, included just 10 tropical populations. Even fewer studies have evaluated resource matching, resource prediction, or economy of scale hypotheses, or otherwise investigated factors that might influence interannual variation in the tropics.

Of those studies at any latitude that have tested economies of scale, most have focused on predispersal processes such as pollination and predispersal seed predation (Table 1). Few studies have tested for postdispersal economies of scale by evaluating annual variation in seedling recruitment relative to annual variation in seedfall, and those few studies indicate that economies of scale are less likely after seeds disperse (Table 1; Fisher Exact Test, $P = 0.029$ for interaction between predispersal insect predator vs. another predator and an economy of scale). There are at least two reasons to expect this outcome. The first concerns differences between pre- and postdispersal predators (Nilsson 1985, Sork 1993). The most important predispersal seed predators tend to be relatively host-specific insects (Janzen 1980). Large host seed crops satiate these insects because, lacking alternative hosts, insect numbers decline when host seed crops are small and because larval development times limit reproductive recruitment before seed dispersal. In contrast, postdispersal predators include a mix of insects, pathogens, and vertebrates. Pathogens and vertebrates are less likely to be satiated because most pathogens are capable of rapid reproductive responses, while most vertebrates have relatively broad diets and are unlikely to decline in numbers when one food source fails. Predispersal predators tend to favor economies of scale, while postdispersal predators do not.

The second reason that economies of scale are unlikely after seeds are dispersed concerns the effects of

interannual variation in seed production on the average local densities of conspecifics experienced by dispersed seeds. Postdispersal performance (survival or growth) is often negatively density dependent or inversely related to the local density of conspecific seeds or seedlings (reviewed by Wright [2002] for tropical forest plants). This raises the possibility that spatial and temporal variation in seedfall density may interact. When all else is equal, negative density dependence insures that seed and seedling performance will be reduced in years characterized by high seedfall density. This is exactly the opposite of an economy of scale. More generally, temporally variable seedfall will increase the local density of conspecific seeds experienced by a representative seed, and this will decrease negatively density-dependent seed performance (see *Introduction: Theory*). This, in turn, sets the stage for selection to act to minimize interannual variation unless negative density dependence is alleviated or seed dispersal is more effective when seed crops are large.

In this study, we document interannual variation in seed production for 108 woody plant species from Barro Colorado Island (BCI), Panama, and evaluate the hypothesis that annual seedfall is less variable on BCI than at higher latitudes. We also document annual variation in seedling recruitment for 32 of these species using spatially explicit data. We use these data to quantify annual and spatial variation in seedfall, to update analyses of density dependence during the seed-to-seedling transition (Harms et al. 2000), to investigate how interannual variation in seedfall interacts with negative density dependence, and to test for economies of scale in seedling recruitment.

Theory

Seedfall varies spatially because of variation in seed production among parent trees, variation in seed dispersal with distance to parent trees, and further spatial variation in seed dispersal due to microhabitat (directed dispersal) and other factors (Nathan and Muller-Landau 2000). Seeds are thus clumped in space, rather than being randomly or evenly distributed. This spatial variation is important because seed survival and seedling establishment are negatively dependent on local conspecific seed density (Harms et al. 2000). As a result, spatial variation in seedfall decreases mean recruitment success per seed in the population as a whole because it increases the mean local density of conspecific seeds experienced by a seed. Similarly, temporal variation in seedfall also increases the perceived local density of conspecific seeds of the same cohort, and thus also decreases recruitment per seed.

We can analytically illustrate how local density dependence interacts with spatial and temporal variation in seedfall. Consider a population with total seed production F , whose seeds land in location x with probability $p(x)$. Then the expected seed density $S(x)$ at location x is simply as follows:

$$S(x) = Fp(x).$$

Assume further that seed survival to recruitment is a power-law function of local expected seed density. Thus, the expected density of recruits, $R(x)$, at location x is

$$R(x) = a[S(x)]^b = aF^b[p(x)]^b$$

where $0 < a < 1$ and $b < 1$, so that survival is negatively density dependent (as shown in Harms et al. 2000 and in the analyses below). We can then obtain the total number of surviving seedlings that year, R_{total} , by integrating over the total area:

$$R_{\text{total}} = \int R(x) dx = F^b a \int [p(x)]^b dx.$$

Note that the total number of recruits scales as F^b times a constant that depends on the parameters of dispersal and density dependence, which we will henceforth denote k .

If seed production is constant among years, then the total number of recruits in T years is simply

$$R_{\text{constant}} = TkF^b.$$

If instead seed production varies among years and is lognormally distributed with distribution $p(F)$, mean log seed production μ , and standard deviation of log seed production σ , then we must integrate over the distribution of seed production to obtain the expected number of seedlings in T years:

$$\begin{aligned} R_{\text{variable}} &= T \int_0^{\infty} R_{\text{total}}(F) p(F) dF \\ &= T \int_0^{\infty} kF^b \frac{1}{F\sigma\sqrt{2\pi}} \exp\left\{-\frac{[\log(F) - \mu]^2}{2\sigma^2}\right\} dF \\ &= Tk \exp\left(b\mu + \frac{b^2\sigma^2}{2}\right). \end{aligned}$$

Because the mean seed production \bar{F} , is $\exp(\mu + (\sigma^2/2))$, this can be rewritten as simply

$$R_{\text{variable}} = Tk\bar{F}^b \exp\left[-\frac{\sigma^2}{2}b(1-b)\right].$$

We can calculate the expected decrease in recruitment due to variable seedfall as the ratio

$$\frac{R_{\text{variable}}}{R_{\text{constant}}} = \exp\left[-\frac{\sigma^2}{2}b(1-b)\right]. \quad (1)$$

Note that this ratio depends only on the strength of density dependence (b) and the magnitude of annual variation in seedfall (σ), and is not sensitive to the form of the seed shadow. This ratio is always less than one when $0 < b < 1$. Moreover, when $0 < b < 1$, the larger the annual variation in seedfall (larger σ), the smaller this ratio and the greater the reduction in recruitment. If there is no density dependence ($b = 1$) or if the

number of recruits is independent of the number of seeds ($b = 0$), then variation in seedfall has no effect. If $b < 0$, that is, if negative density dependence is so extreme that the number of recruits decreases as the number of seeds increases, then increased annual variation in seedfall leads to increased recruitment. Intuitively, when $b < 0$, gains in recruitment in years of very low seedfall more than offset losses in recruitment in years of very high seedfall, relative to cumulative recruitment when all years have intermediate seedfall. Such overwhelming negative density dependence could lead to selection for low seedfall in all years (possibly with freed resources allocated to seed/seedling defense), but not to selection for more variable seedfall, because years of high seedfall would bring only fewer recruits at a higher cost. Data and theory both suggest that b values are unlikely to be negative (Hubbell 1980, Harms et al. 2000). Thus, variable annual seedfall and negatively density-dependent, postdispersal seed survival are most likely to interact to reduce numbers of recruits.

This simple analysis succinctly illustrates how variable fecundity reduces recruitment when postdispersal seed survival is negatively density dependent and dispersal and density dependence act identically in years of high and low seedfall. We will calculate the expected decrease in seedling recruitment due to observed annual variation in seedfall given observed levels of density dependence and spatial variation in the probability of seed arrival, and assess whether variation in density dependence among years of high and low seedfall could compensate for this handicap. We analyze seed dispersal distances, including variation in dispersal distances among years, elsewhere (Dalling et al. 2002, Muller-Landau et al. 2002, *in press*).

METHODS

Study site

Annual rainfall averages 2600 mm and supports semideciduous tropical forest on BCI (9°10' N, 79°51' W) (Windsor 1990). This study was conducted in a 50-ha Forest Dynamics Plot, where all trees and shrubs >1 cm in diameter at breast height have been mapped and identified (Condit 1998). Humans have had little impact on this forest since at least 1500 BP (Piperno 1990), with the exception of a small (<2 ha) patch of secondary forest perhaps 120 years old. BCI has a diverse, and, with the exception of macaws (*Ara* spp.) and white-lipped peccaries (*Tayassu pecari*), intact community of vertebrate seed dispersers, seed predators, and seedling herbivores. Because of a well-enforced ban on hunting, densities of mammalian herbivores are comparable with those at much more remote sites (Wright et al. 1994, Peres 1996, Wright et al. 2000).

Seed and recruit censuses

The rain of seeds and flowers was censused weekly from 1 January 1987 through 21 May 2003, using 200

seed traps set along 2.7 km of trails within the 50-ha plot (Wright and Calderón 1995, Wright et al. 1999). Each seed trap consisted of a square, 0.5-m² PVC frame supporting a shallow, open-topped, 1-mm mesh bag, and suspended 0.8 m above the ground on four PVC posts. Traps were located at 13.5-m intervals on alternating sides of the trail and randomly between 4 and 10 m from the trail so that distances between the nearest traps averaged 18.9 ± 3.6 m (mean \pm 1 SD). All flowers, seeds, fruits, capsules, and other reproductive parts of plants that fell into the traps were identified to species and counted (only presence was recorded for flowers). Fruits and seeds were further categorized as aborted, immature, mature (endosperm-filled), or damaged by insects or vertebrates. For each species, the number of undamaged, mature fruit was multiplied by the species-specific average seed-to-fruit ratio and added to the number of undamaged seeds to estimate the total number of viable seeds falling into each trap.

All woody seedlings <50 cm tall in 600 1-m² seedling plots were censused between January and March each year from 1994 through 2003 (Harms et al. 2000, Wright 2002). Seedling plots were located 2 m from the three sides of each seed trap away from the nearby trail. Henceforth, "station" will refer to a seed trap and its three associated seedling plots. Each seedling was tagged and identified when it was first censused, and measured (height and number of leaves) every year. The analyses here consider seedlings only when they first enter, or recruit into, the census. The age of seedlings at recruitment varies among species due to differences in the timing of seedfall and different lag times until germination (see *Discussion: Spatial density dependence*).

Criteria to include species

We considered only trees, shrubs, and lianas; other life forms were excluded. We also excluded species whose seeds passed through the 1-mm mesh (*Cecropia*, *Conostegia*, *Marcgravia*, *Miconia*, *Mikania*); species whose seeds could not be reliably identified to species (*Ficus*, *Inga* excepting *I. marginata*, *Zanthoxylum panamense* and *Z. procerum*, *Abuta racemosa* and *Chondrodendron tomentosum*); and the single species that reproduced twice each year (*Hyeronima alchorneoides*).

We included only species for which we could be confident that the 200 stations monitored a minimum of four seed-bearing individuals. The locations of traps, the number of seeds captured, and the presence of flowers were compared with the locations and sizes of all conspecific trees and shrubs present in the 50-ha plot. Discrete clusters of trees and traps were identified, where each cluster included one or more traps that captured both flowers and seeds located near a large conspecific that was presumed to bear seeds and where clusters were separated by two or more traps that failed to capture conspecific flowers. We included tree and

shrub species represented by four or more clusters and presumably by four or more seed-bearing adults located above a station. These species were each represented by many more reproductively sized individuals in the 50-ha plot that were not directly over a census station so that the 200 stations collectively monitored a larger population.

Lianas are not mapped in the 50-ha plot, necessitating a different criterion to ensure that a population of individuals was being monitored. Each tree and shrub species represented by four or more discrete clusters of traps (see previous paragraph) also had seeds or fruit captured in 10 or more traps in at least one year. We therefore included liana species captured in 10 or more traps in at least one year to maintain consistent criteria across life forms.

Finally, we also excluded species with fewer than 75 seeds plus fruit captured during 15 annual reproductive events. For each species, the month of minimum seedfall defined start and end dates of annual reproductive events. After 15 yr, cumulative seedfall was zero for at least one month for every species examined here. The first reproductive event started in 1987 and the 15th ended in 2002 for each species.

Recruitment was evaluated for species with seedling recruits recorded at 30 or more stations in nine years, 10 or more recruits recorded for at least one station in at least one year, and seeds or fruit recorded for 50 or more stations for the appropriate nine years. For seedlings, the nine years included 1995 through 2003, because new recruits could not be distinguished during the initial 1994 seedling census. The timing of seedfall, species-specific germination lags (Garwood 1983), and the timing of the annual seedling census were incorporated to associate recruits with the appropriate estimate of annual seedfall. The 1998 fruiting of *Dipteryx panamensis* will illustrate this association. No seeds of *D. panamensis* have ever fallen into traps in July, the mean date for seed dispersal is in January, and seeds germinate in May and June. Seedfall occurring largely during January and February 1998 (recorded from 16 July 1997 through 15 July 1998) led to germination in May and June 1998 and to recruits first recorded between January and March 1999. Thus, our seed-to-seedling transition spans 11–13 months for *D. panamensis*, including 4 months of postdispersal exposure of seeds and 7–9 months of postgermination exposure of seedlings. The seed-to-seedling transition can be much shorter for other species (see *Discussion: Spatial density dependence*).

Annual and spatial variation in seedfall

To quantify annual variation (CV_{years}), coefficients of variation were calculated using seedfall averaged over the 200 seed traps for each annual reproductive event (Kelly 1994). Skewness and kurtosis were evaluated for both untransformed and log-transformed values of annual seedfall for each species. To quantify spatial

variation (CV_{traps}), coefficients of variation were calculated using seedfall averaged over the 15 years for each seed trap.

Mann-Whitney *U* tests were used to evaluate the hypothesis that CV_{years} differed between plant species from BCI and those from extratropical latitudes. Shibata et al. (2002) used similar methods (121 0.5-m² seed traps in a regular grid over a 1.2-ha plot) to document seedfall for nine years and 14 temperate tree species from the Ogawa Forest, Japan. A second comparison was made using extratropical populations taken from the literature review of Herrera et al. (1998). Only those populations with seedfall recorded for 12–18 years were used because this brackets the 15 years recorded for BCI, and variation tends to increase with the length of ecological time series (Pimm and Redfearn 1988).

Relationships between seedfall and recruitment

An initial analysis explored the relationship between stand-level recruitment and stand-level seedfall for the nine years. Let \bar{R}_t and \bar{S}_t represent mean recruit and mean seedfall density taken over the 200 stations for year *t*, respectively. Stepwise multiple regression was used to evaluate the following quadratic equation:

$$\bar{R}_t = c_0 + c_1\bar{S}_t + c_2\bar{S}_t^2 \quad (2)$$

where c_0 , c_1 and c_2 are fitted coefficients. An economy of scale is realized if \bar{R}_t is an accelerating function of \bar{S}_t , that is, if the second-order coefficient, c_2 , is significant and positive and the first-order coefficient, c_1 , is insignificant or significant and positive. This stand-level analysis most closely approximates earlier studies that compared annual seedfall and recruitment (Hett 1971, Jensen 1985, Crawley and Long 1995).

We then pooled data from all stations and all year cohorts to describe the overall relationship between local recruit and seedfall density for each species. Let S_{it} and R_{it} represent the density of seeds and conspecific recruits for station *i* and year *t*, respectively. We used maximum likelihood methods to compare the following functions:

$$\text{linear} \quad R_{it} = aS_{it} \quad (3a)$$

$$\text{exponential} \quad R_{it} = aS_{it}e^{-bS_{it}} \quad (3b)$$

$$\text{power} \quad R_{it} = aS_{it}^b \quad (3c)$$

using both Poisson and negative binomial error distributions. Model selection is unaffected by data values with $S_{it} = R_{it} = 0$ because their likelihood equals one under all models. Data values with $S_{it} < R_{it}$ or $S_{it} = 0 < R_{it}$ do present a problem, however, because they are infinitely unlikely and thus their likelihood functions are undefined under the Poisson and negative binomial error distributions, respectively. HilleRisLambers et al. (2002) simply set S_{it} equal to R_{it} whenever $S_{it} < R_{it}$ in a similar analysis. We adopted their convention even

though it introduces a conservative bias against detecting negative density dependence by systematically increasing seedfall density whenever observed seedfall fell below observed recruit density. The negative binomial error distribution invariably provided a significant improvement over the Poisson error distribution. This was expected given the large variation associated with clumped seed dispersal, and fits with the Poisson error distribution were not considered further. The exponent b differs significantly from one (zero) when the power (exponential) function provides a significantly better fit than the linear function, and this outcome is consistent with density-dependent survival during the seed-to-seedling transition. Asymptotic standard errors and Wald confidence intervals were used to determine whether b values differed significantly from zero for power function fits.

Two analyses were performed to evaluate how recruitment responded to simultaneous spatial and temporal variation in seedfall. The first quantified the potential consequences of temporal variation in seedfall for recruitment given the observed negative density dependence (see *Introduction: Theory*). We did not use Eq. 1 for this purpose because it only incorporates log-normal variation in seed production. Instead, we used a numerical analog of Eq. 1 that incorporates all observed temporal variation. Let p_i represent the proportion of seeds arriving at station i over T years, let F_t be the seed production in year t , let \bar{F} be the mean annual seed production, and assume the relationship between recruit and seedfall density, $R(S)$, is unchanging and equals the function selected using the methods described in the previous paragraph. Then the number of recruits expected at I stations over T years of constant seedfall is

$$R'_{\text{constant}} = T \sum_{i=1}^I R(\bar{F}p_i) \quad (4)$$

and the number of recruits expected given annually variable seedfall and the same spatial pattern of seed rain is

$$R'_{\text{variable}} = \sum_{t=1}^T \sum_{i=1}^I R(F_t p_i). \quad (5)$$

The empirically determined ratio $R'_{\text{variable}}:R'_{\text{constant}}$ quantifies the potential consequences of observed variable seed production for recruitment given observed spatial variation in seedfall density and an unchanging function for seed-to-seedling survival.

The final analysis used maximum likelihood methods to determine whether the spatial relationship between recruit and seedfall densities varied among years. The single year of highest seedfall was contrasted with the eight pooled years of lower seedfall, unless seedfall for a second year fell within 10% of seedfall in the highest year, in which case the two pooled years of highest seedfall were contrasted with the seven pooled years

of lower seedfall. The following models with different combinations of year-dependent parameters were compared (only power functions were used because these proved significantly better than exponential or linear functions for all species):

intercepts and exponents in common,

$$R_{it} = aS_{it}^b \quad (6a)$$

intercepts in common, exponents different,

$$R_{it} = \begin{cases} aS_{it}^{b_h} & \text{if } t \text{ is a high seedfall year} \\ aS_{it}^{b_l} & \text{otherwise} \end{cases} \quad (6b)$$

intercepts different, exponents in common,

$$R_{it} = \begin{cases} a_h S_{it}^b & \text{if } t \text{ is a high seedfall year} \\ a_l S_{it}^b & \text{otherwise} \end{cases} \quad (6c)$$

both intercepts and exponents different,

$$R_{it} = \begin{cases} a_h S_{it}^{b_h} & \text{if } t \text{ is a high seedfall year} \\ a_l S_{it}^{b_l} & \text{otherwise.} \end{cases} \quad (6d)$$

Analyses

The Akaike Information Criterion (AIC) was used to select the best model from among the models described by Eqs. 3a–c and 6a–d (note that Eqs. 3c and 6a are identical). AIC is calculated as $-2L + 2P$, where L is the log likelihood of the model and P is the number of parameters. We tabulated the difference (ΔAIC) between the AIC value observed for each model and the smallest AIC value observed for that same species following the recommendation of Burnham and Anderson (1998). If this difference exceeds 10 for two models, then there is no empirical support for the model with the larger AIC value. If this difference is less than two, then the two models cannot be distinguished (Burnham and Anderson 1998).

We also compared the models described by Eqs. 3 and 6 in a hypothesis-testing mode. Less parsimonious models with additional parameters were evaluated relative to more parsimonious models with fewer parameters using likelihood ratio tests (chi-squared tests on the differences in log likelihoods between the models, with degrees of freedom determined by the differences in the number of parameters (Hilborn and Mangel 1997)). This approach has the twin advantages that it is familiar to more ecologists and the sequential Bonferroni procedure (Rice 1989) can be used to protect against Type II error when multiple tests are performed, and the disadvantage that it cannot be used to compare models with the same number of parameters. The sequential Bonferroni procedure was also applied to analyses of the quadratic relationship between annual recruitment and annual seedfall (Eq. 2). Two-tailed tests were used throughout. Analyses were performed with SYSTAT 10.0 (SPSS 2000).

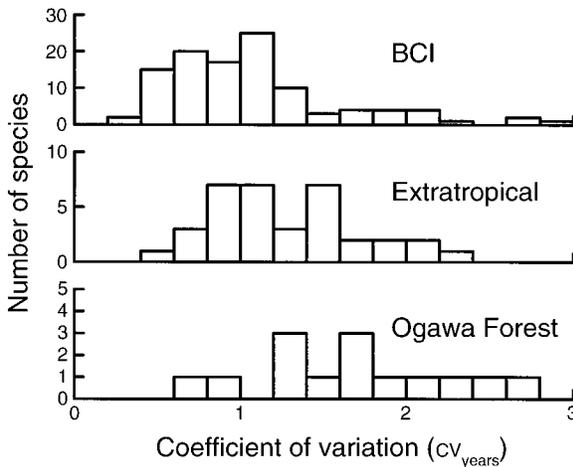


FIG. 1. Frequency histograms of coefficients of variation for seedfall density recorded for 15 years and 108 species from Barro Colorado Island, Panama (this study); for 12–18 years and 35 populations from extratropical latitudes (Herrera et al. 1998); and for 9 years and 14 tree species from the Ogawa Forest, Japan (Shibata et al. 2002).

RESULTS

Annual and spatial variation in seedfall

The 200 seed traps collected 960 872 undamaged seeds and fruits representing 494 species in 853 weekly censuses between 1 January 1987 and 21 May 2003. Six shrub, 59 tree, and 43 liana species fulfilled the criteria to be included in analyses of seedfall (Appendix A). The 15 annual values of seedfall were significantly skewed (kurtotic) for 62 (48) of these 108 species. All significant values of skewness and kurtosis were positive for untransformed values of seedfall, which indicates a long tail of large values. When annual seedfall was log transformed, the number of significantly skewed (kurtotic) species was just 16 (10). Distributions of annual seedfall were approximately lognormal for most species.

The median coefficient of variation (cv_{years}) of annual seedfall was 1.01 for the 108 BCI populations (Fig. 1). cv_{years} was significantly larger for 35 extratropical plant populations and also for 14 tree populations from the Ogawa Forest, Japan (Fig. 1, Mann-Whitney U tests, $P < 0.01$ and $P < 0.001$, respectively). Spatial variation in seedfall among traps (cv_{traps}) was greater than temporal variation in seedfall among years (cv_{years}) for every BCI species (Fig. 2).

Relationships between seedfall and recruitment

The 600 seedling plots included 29 312 recruits representing 282 species in nine annual censuses between 1995 and 2003. Three shrub, 16 tree, and 13 liana species fulfilled the criteria to be included in analyses of recruitment (Appendix B). A quadratic model (Eq. 2) was used to evaluate the stand-level relationship between annual recruitment and seedfall. The first-order

coefficient (c_1) was always positive when significant. The second-order coefficient (c_2) was significant and positive for eight species after the sequential Bonferroni correction. Realized recruitment per seed increased with annual seedfall for these eight species (Fig. 3).

Power functions (Eq. 3c) best described the relationship between local recruit and seedfall densities for all 32 species when the nine-year cohorts were pooled. Power functions provided significantly better fits than linear functions (Table 2, minimum $\Delta AIC = 23.52$; minimum likelihood ratio test $\chi^2 = 19.72$, $P < 0.001$ after the sequential Bonferroni correction) and substantially better fits than exponential functions for all species (Table 2, minimum $\Delta AIC = 20.90$). The exponent (b) of the best fit power function was significantly less than one for all 32 species. The test based on asymptotic standard errors further indicated that b values were significantly greater than zero for 11 species and significantly smaller than zero for no species. Sample size was important for the latter test. Numbers of recruits and seeds were significantly greater for the 11 species with positive b values than for the 21 species whose b values were indistinguishable from zero (Mann-Whitney U tests, $P < 0.001$ and $P < 0.01$, respectively). We believe that b values will prove to fall between zero and one for ever more species as we accumulate additional years of data and sample size increases. To summarize, significant negative density dependence characterized the seed-to-seedling transition for every species; nonetheless recruit density tended to increase with seedfall density (Harms et al. 2000).

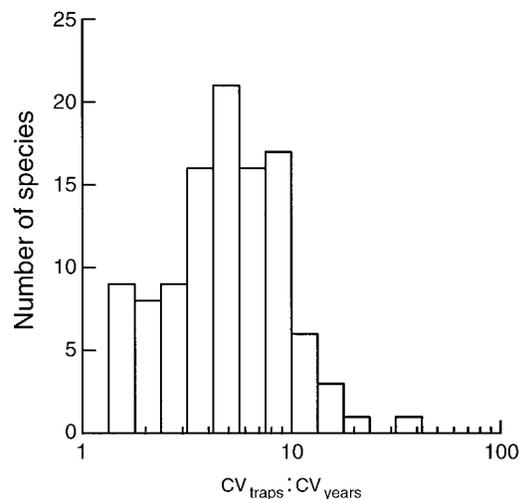


FIG. 2. The ratio of temporal (cv_{years}) to spatial (cv_{traps}) variation in seedfall for 59 tree, 43 liana, and 6 shrub species. Temporal variation is represented by the coefficient of variation of annual seedfall summed over 200 traps for each of 15 years. Spatial variation is represented by the coefficient of variation of seedfall summed over 15 years for each of 200 traps.

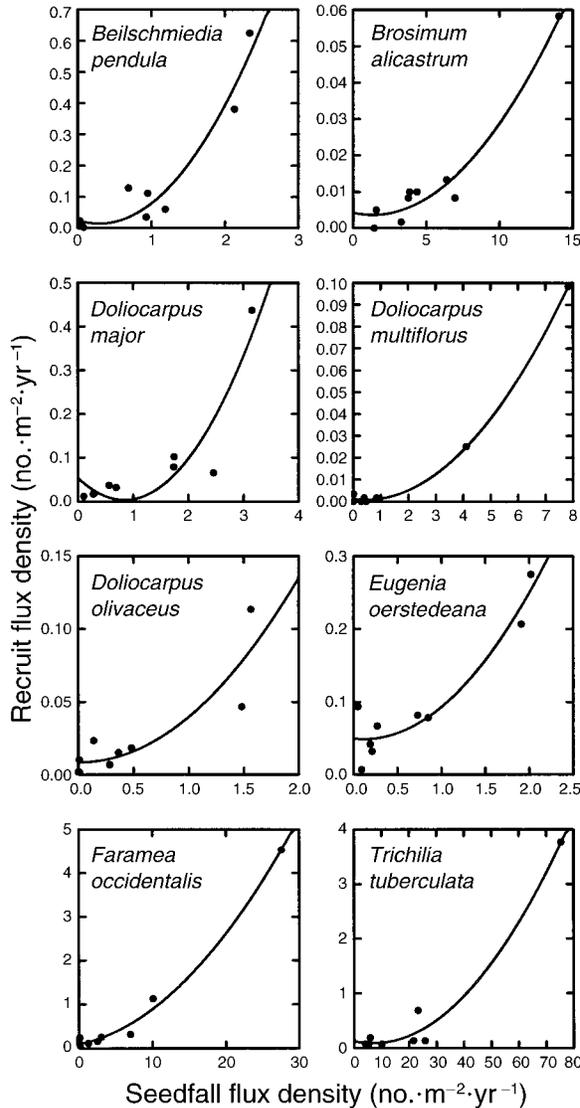


FIG. 3. Mean recruit and seedfall flux densities for nine years (with means taken over 200 census stations), and the best-fit quadratic functions (Eq. 2), for the eight BCI species that realized an economy of scale after seed dispersal. Recruits are seedlings that are known to have germinated and recruited within the past year.

The ratio $R'_{\text{variable}}:R'_{\text{constant}}$ (Eq. 5:Eq. 4) quantifies the potential consequences of variable seedfall for recruitment given observed spatial variation in seedfall density and an unvarying function for density-dependent survival during the seed-to-seedling transition. This ratio was less than one for 29 of the 32 species evaluated (Fig. 4). The three exceptional species had estimated b values < 0 for Eq. 3c. Although $R'_{\text{variable}}:R'_{\text{constant}} > 1$ is expected when b values are negative, there are reasons to doubt whether negative density dependence actually takes this extreme form (see *Introduction: Theory* and previous paragraph). We conclude that variable annual seedfall will tend to reduce recruitment given

observed spatial variation in seedfall density if negatively density-dependent survival acts identically across years.

The final analysis contrasted the relative strength of density dependence during the seed-to-seedling transition in the year(s) of greatest seedfall and in the remaining years of lower seedfall (Eqs. 6). Survival during the seed-to-seedling transition was significantly larger for the year(s) of greatest seedfall than for the remaining years of lower seedfall for 12 species when the sequential Bonferroni procedure was applied to likelihood ratio tests (Table 2). This included the eight species in Fig. 3 and also *Hirea reclinata*, *Pouteria reticulata*, *Psychotria horizontalis* and *Simarouba amara*. The exponent (b value) alone was significantly larger for 10 species (Eq. 6b), the intercept alone was significantly larger for *Faramea occidentalis* (Eq. 6c), and both the intercept and exponent were significantly larger for *Trichilia tuberculata* (Eq. 6d). Fig. 5 presents the relationship between recruit and seedfall densities for 4 of these 12 species. Finally, the b value was significantly smaller for the year(s) of greatest seedfall than for the remaining years of lower seedfall for *Macfadyena unguis-cati* and *Randia armata* (Table 2). To summarize, survival during the seed-to-seedling transition was significantly larger in the year(s) of greatest seedfall for 12 species, and significantly smaller for 2 species.

DISCUSSION

Annual and spatial variation in seedfall

Annual variation in seedfall on BCI was substantial ($CV_{\text{years}} > 1$ for 50% of species), but was still significantly smaller than for higher latitudes (Fig. 1). The BCI-Ogawa forest comparison is particularly compelling because both studies used seed traps located independently of seed-bearing trees to quantify seedfall so that both studies sampled the more abundant and fecund species at their respective sites. The BCI data support the hypothesis that annual variation in seedfall is lower in the tropics than at higher latitudes (Kelly and Sork 2002). There is, however, ample evidence that CV_{years} varies geographically within both the tropics (e.g., greater for the Dipterocarp forests of Southeast Asia) and at higher latitudes (e.g., greater for New Zealand). Additional seedfall studies from the tropics will be required to substantiate a tropical-extratropical dichotomy and to evaluate possible causes.

Spatial variation in seedfall density was greater than annual variation for all 108 BCI species (Fig. 2). The rarity of seed-bearing adults, variation in seed deposition with distance, and clumped seed deposition by frugivores are the most important sources of this spatial variation (Muller-Landau 2001, Muller-Landau et al. 2002). Spatial variation in seedfall density sets the stage for density-dependent performance.

TABLE 2. Species, life forms, sample sizes, model selection criteria, and parameters from the best-fit model to describe the relationship between recruit and seedfall density.

Species	Life form	No. seeds	No. recruits	Difference from minimum Akaike Information Criterion for model		
				3a	3b	3c or 6a
<i>Beilschmiedia pendula</i> †	T	870	822	53.00	52.00	30.16
<i>Brosimum alicastrum</i>	T	4870	69	154.98	147.88	71.40
<i>Chrysophyllum cainito</i>	T	479	132	47.78	43.24	0
<i>Dolioscarpus major</i> †	L	1342	478	197.02	183.58	66.18
<i>D. multiflorus</i>	L	1456	78	47.82	45.88	10.86
<i>D. olivaceus</i>	L	455	142	99.96	95.32	34.04
<i>Eugenia oerstediana</i>	T	903	529	264.12	210.90	33.78
<i>Fareamea occidentalis</i> †	T	5506	4143	501.76	446.16	275.28
<i>Guapira standleyanum</i>	T	419	99	88.92	41.24	0
<i>Heisteria concinna</i>	T	503	187	74.66	63.28	1.98
<i>Hippocratea volubilis</i>	L	1015	227	128.48	111.58	0
<i>Hiraea reclinata</i>	L	933	258	218.08	169.20	24.18
<i>H. faginea</i>	L	247	129	24.46	20.90	6.34
<i>H. grandifolia</i>	L	329	128	45.76	44.62	3.36
<i>Hybanthus prunifolius</i> †	S	9231	2781	386.78	293.54	3.84
<i>Jacaranda copaia</i> †	T	64 713	116	23.52	77.4	0
<i>Macfadyena unguis-cati</i>	L	436	150	98.28	83.98	14.70
<i>Maripa panamensis</i>	L	478	359	200.90	143.10	0
<i>Mascagnia hippocrateoides</i> †	L	1144	626	60.08	44.88	0
<i>M. nervosa</i> †	L	17 978	1042	281.92	248.08	3.00
<i>Paragonia pyramidata</i>	L	771	202	71.44	54.24	5.66
<i>Pouteria reticulata</i> †	T	349	202	101.06	81.76	10.18
<i>Prionostemma aspera</i>	L	244	131	55.96	41.52	0
<i>Psychotria horizontalis</i>	S	1028	768	325.04	271.34	10.86
<i>Quararibea asterolepis</i>	T	16 473	866	391.38	345.94	3.2
<i>Randia armata</i> †	T	3227	1637	184.26	165.18	10.92
<i>Simarouba amara</i>	T	773	68	56.62	54.70	18.64
<i>Sorocea affinis</i>	S	387	363	216.02	158.52	0.16
<i>Tetragastris panamensis</i> †	T	2248	380	78.88	71.20	0
<i>Thinouia myriantha</i>	T	7804	309	284.16	240.48	5.24
<i>Trichilia tuberculata</i> †	T	17 659	3097	786.80	763.16	458.28
<i>Triplaris cumingiana</i>	T	455	93	58.86	52.34	0

Notes: Life forms are tree (T), liana (L), and shrub (S). Numbers of seeds and recruits are summed over nine years and 200 0.5-m² seed traps and 600 1-m² seedling plots, respectively. Model selection criteria are differences between the values of the Akaike Information Criterion observed for each model and the minimum (best) AIC observed for the six models under consideration (Δ AIC). Models are identified by equation numbers (see *Methods: Relationships between seedfall and recruitment*). Parameter values are from the best-fit model as determined by likelihood ratio tests after sequential Bonferroni correction: a single value is presented for *a* and *b* if model 3c (or 6a) provided the best fit; separate values are presented for years of low (subscript l) and high (h) seedfall if models 6b, 6c, or 6d provided the best fit. Models 3a and 3b never provided the best fit.

† The *b* value was significantly greater than zero for model 3c. All *b* values were significantly less than 1.

Spatial density dependence

We evaluated density dependence during the seed-to-seedling transition. The duration of this transition varied among species due to the timing of seedfall and germination. For example, the transition includes four months between seedfall and germination and seven to nine months after germination for *Dipteryx panamensis* (see *Methods: Relationships between seedfall and recruitment*). At the other extreme, the transition includes a few days between seedfall and germination and two to five months after germination for *Trichilia tuberculata*. These differences necessitate caution when interpreting interspecific comparisons; however, the intraspecific comparisons among years conducted here are unaffected.

Analytical methods influence the frequency with which density dependence is detected (HilleRis-Lambers et al. 2002). Two different analyses have now

been used to evaluate density dependence during the seed-to-seedling transition, with the same outcome for BCI. Visual inspection of the data, linear regression analyses, and maximum-likelihood analyses all indicate that power functions, with exponents indicative of negative density dependence, describe the relationship between conspecific recruit and seedfall density for every BCI species examined (Fig. 5, Table 2; Harms et al. 2000).

Negative density dependence enhances species coexistence in spatially structured plant communities (Chave et al. 2002). Pervasive negative density dependence characterizes postdispersal seed survival on BCI (Fig. 5, Table 2). Negative density dependence continues to characterize growth and survival as seedlings mature and even large saplings are affected in tropical forests (reviewed by Wright 2002). The full consequences for tree demography and species coexistence

TABLE 2. Extended.

Difference from minimum Akaike Information Criterion for model			Power function parameters			
6b	6c	6d	$a(a_1)$	a_h	$b(b_1)$	b_h
0.84	2.18	0	0.532		0.428	0.825
0	45.00	0.12	0.616		-0.743	0.244
1.26	1.12	3.06	0.663		0.169	
0	22.72	1.60	0.814		-0.016	0.540
0	3.92	1.92	0.773		-0.227	0.234
0	20.12	1.70	0.929		-0.428	0.277
0	13.26	1.70	1.083		-0.074	0.270
38.88	2.26	0	0.943	5.042	0.285	
0.90	1.32	2.90	1.014		-0.239	
0	0.32	1.64	0.738		0.176	
0.60	2.00	1.42	1.068		0.012	
0.10	15.44	0	1.092		-0.369	0.048
0	6.86	0.70	0.761		0.305	
0	4.86	0.12	0.889		0.164	
0	2.14	1.34	0.985		0.312	
1.40	1.80	2.58	0.014		0.360	
1.02	0	0.98	0.952		0.075	-0.504
2.00	1.88	3.80	1.030		0.076	
1.60	0.76	2.38	0.859		0.440	
0	0.30	1.88	0.196		0.383	
0.54	0	1.54	0.584		0.229	
0	4.10	1.52	0.999		-0.043	0.292
1.74	1.96	3.52	0.834		0.075	
0	7.82	1.98	1.324		0.002	0.262
2.64	0	1.68	0.806		0.087	
0	5.44	1.74	1.219		0.474	0.250
1.72	0	0.06	0.505		-0.252	0.353
0.68	0	1.92	1.115		-0.007	
0.82	1.50	2.68	0.659		0.277	
0	2.94	1.54	0.288		0.109	
47.50	22.66	0	0.487	1.928	0.180	0.417
1.98	1.58	2.96	0.618		0.187	

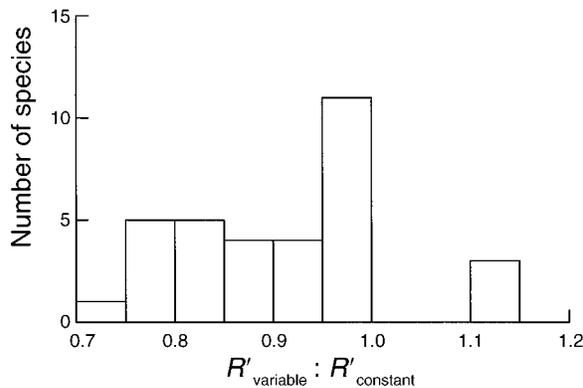


FIG. 4. Frequency histogram of the ratio of the number of seedling recruits expected given variable seedfall (Eq. 5) to the number expected given constant seedfall (Eq. 4) for 16 tree, 13 liana, and three shrub species from Barro Colorado Island, Panama. Temporally variable seedfall and subsequent density-dependent seed survival have the potential to reduce recruitment when the ratio $R'_{variable} : R'_{constant}$ is less than 1. These values incorporate observed spatial variation in seedfall density and assume that density-dependent seed survival acts identically across years (see *Methods: Relationships between seedfall and recruitment*).

will be underappreciated until density-dependent effects are integrated over all life history stages (Alvarez-Buylla 1994).

Implications for variable seed production

Variable annual seedfall and negatively density-dependent, postdispersal seed survival will combine to reduce numbers of recruits when seed dispersal and density dependence act identically across years (see *Introduction: Theory*). This reduction can be substantial, with variable seedfall resulting in excess negatively density-dependent mortality of up to 28% of the recruits expected if seedfall were constant across years (Fig. 4). This handicap must be overcome for larger seed crops to realize greater per seed recruitment after dispersal (a postdispersal economy of scale) and for selection acting after dispersal to favor more variable annual seedfall.

The handicap was overcome for the eight species for which per seed recruitment increased with seed crop size (Fig. 3). We could not identify any traits that set these species apart: they were not distinguished by significantly higher or lower annual or spatial variation in seedfall, or seed mass (Kruskal-Wallis tests). These eight species plus four additional species exhibited

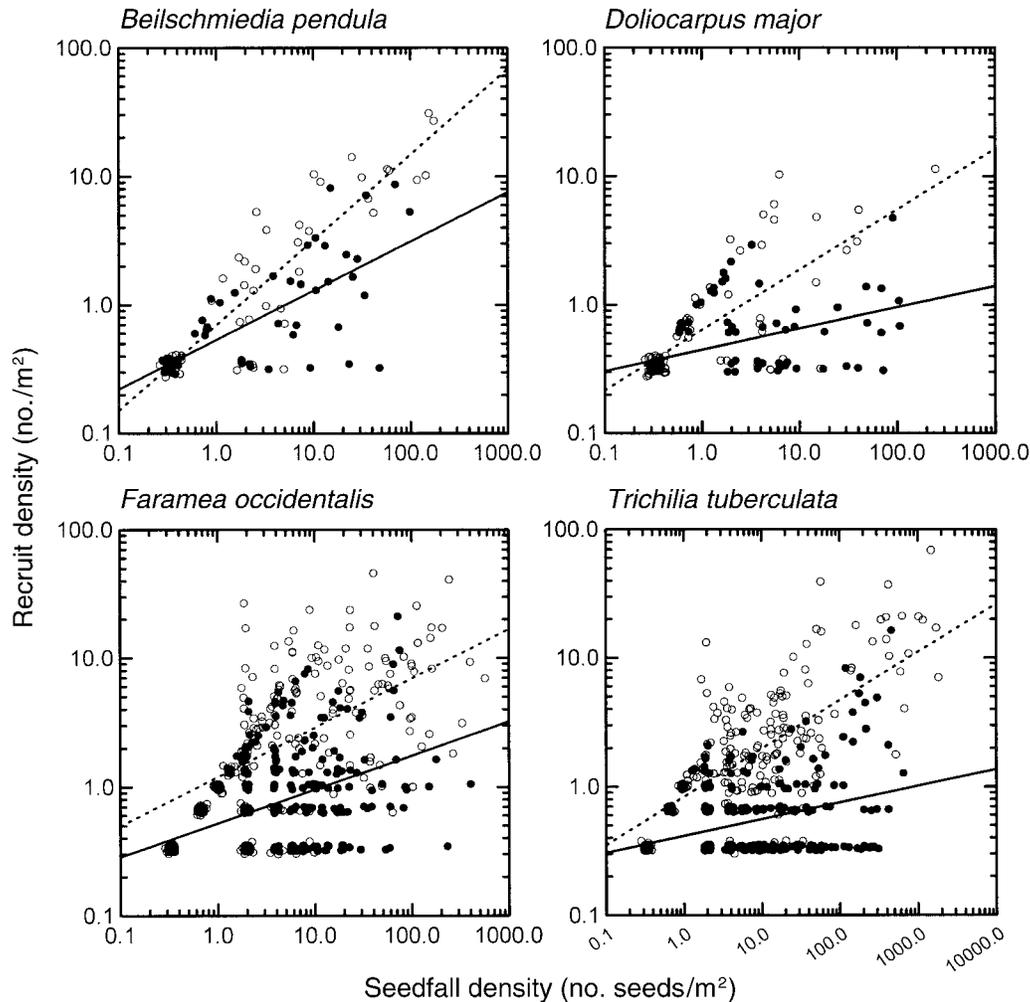


FIG. 5. Survival during the seed-to-seedling transition was significantly larger during the year(s) of greatest seedfall (open circles, dashed line) than during years of lower seedfall (solid circles, solid line) for 12 species from Barro Colorado Island, Panama (just four are shown). The lines represent best-fit power functions determined using maximum-likelihood methods (note the log-log scale). Survival was significantly smaller during the year(s) of greatest seedfall for an additional two species (not shown).

weaker density dependence when seed crops were largest; however, two other species exhibited stronger negative density dependence when seed crops were largest (Table 2).

To summarize, per seed recruitment was significantly greater when seed crops were largest for 12 species, significantly lower for 2 species, and the null hypothesis could not be rejected for 18 species. Published studies provide similar numbers (4:1:3, species, respectively; Table 1), given the bias against publication when the null hypothesis is accepted. Collectively, these studies suggest that the frequency of postdispersal economies of scale is low at least in part because the impact of negative density dependence is enhanced when seedfall varies among years. Additional studies of annual variation in seedfall and postdispersal seed fate will be required to evaluate this tentative conclusion.

Mechanisms contributing to postdispersal economies of scale

At least four mechanisms could contribute to postdispersal economies of scale. Large seed crops might attract disproportionate numbers of frugivores leading to greater seed dispersal and hence greater seed survival (Vander Wall 2002). Alternatively, large seed crops might satiate postdispersal seed or seedling predators, thereby improving survival (Jensen 1985, Nilsson and Wästljung 1987, Crawley and Long 1995, Wolff 1996). A third possibility hinges on predispersal pollinator activity causing an apparent postdispersal economy of scale. Outcrossing often enhances seed and seedling performance. If large flower displays led to increased levels of outcrossing, then per-seed recruitment might increase with seed crop size as a consequence of outcrossing rather than with events that occur during or after seed

dispersal. Finally, successful resource prediction could also lead to an apparent economy of scale because seeds produced in larger numbers in years characterized by conditions favorable for seedling establishment recruit in disproportionately larger numbers. All four mechanisms will lead to greater recruitment per dispersed seed when seedfall is greater (Fig. 3).

The form of density dependence in years with large and small seed crops may help discriminate among these four mechanisms (Fig. 5). Specialized natural enemies are a primary cause of negatively density-dependent seed survival (Janzen 1970). Weaker negative density dependence, as reflected by a greater slope of the relationship between recruits and seeds, is consistent with satiation of enemies. Higher quality, outcrossed seeds, or improved conditions for establishment are more likely to increase survival everywhere (increased intercept a), while leaving the strength of density dependence (the slope, or more strictly the exponent, b) unchanged. Better dispersal should insure that fewer seeds experience high densities of conspecifics (no effect on the density-dependent relationship), and may take seeds to better sites where resources are enhanced (increasing the intercept), but also seems likely to have little impact on the slope. The frugivore attraction hypothesis can be further discounted because dispersal distances tend to be lower in years of high seedfall for the majority of animal-dispersed species on BCI (Muller-Landau 2001). We conclude that the most likely explanation for the economies of scale observed in this study is that some unknown postdispersal pest of seeds or seedlings is partially satiated in the year(s) of greatest seedfall.

Conclusions

Kelly (1994) suggested that $CV_{\text{years}} > 1$ characterizes mast fruiting. Fifty-four of 108 BCI species satisfy this criterion (Fig. 1). The only other reports of mast fruiting from the tropics are for single species that dominate extensive forest stands (Newbery 1998), or for trees from the family Dipterocarpaceae that dominate many forests in Southeast Asia (Curran et al. 1999). Dominance is absent from the forests of BCI, where $CV_{\text{years}} > 1$ characterizes several species with less than one reproductive adult per hectare. Such rare species are unlikely to attract disproportionate numbers of mutualists or satiate their pests independently of the rest of the plant community; however, interspecific synchrony in reproductive effort among species may allow rare species to benefit from community-level satiation of generalist pests on BCI (Wright et al. 1999).

Most studies of annual variation in reproductive effort in plants have focused on predispersal stages (Herrera et al. 1998, Kelly and Sork 2002). All else equal, negative density dependence, which is widespread among plants after seeds are dispersed (Harms et al. 2000, HilleRisLambers et al. 2002, Wright 2002), will reduce recruitment as annual variation in seedfall in-

creases (Eq. 1). This increased mortality will tend to offset predispersal advantages that may be associated with annual variation in reproductive effort. Thus, our understanding of the evolution of temporal variation in seed production will only be complete when its ecological consequences have been evaluated and integrated across reproductive stages (flowers, predispersal seed development, and postdispersal seed fate) for the same plant populations. Such studies have yet to occur (Kelly and Sork 2002).

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APPENDIX A

A table showing annual seedfall for 108 species from Barro Colorado Island, Panama is available in ESA's Electronic Data Archive: *Ecological Archives* E086-044-A1.

APPENDIX B

A table showing annual number of seedling recruits for 32 species from Barro Colorado Island, Panama is available in ESA's Electronic Archive: *Ecological Archives* E086-044-A2.